

## **Attraction of Mexican Fruit Flies (Diptera: Tephritidae) to Grapefruit: Enhancement by Mechanical Wounding of and Experience with Grapefruit**

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*Wild strain, mated, female Mexican fruit flies, *Anastrepha ludens* (Loew), with no prior experience with fruit (naïve), were not attracted to grapefruit, a preferred cultivated host, in wind tunnel experiments. Naïve, mated laboratory strain females were attracted. Prior experience with grapefruit increased attraction of both laboratory and wild strains. More females were attracted to fruit with peel damage than to undamaged fruit, indicating that fruit odor mediated attraction. More naïve than experienced females attempted to oviposit on the sides of the wind tunnel. Experienced laboratory males, but not wild males or naïve males, were attracted to grapefruit. Attraction and oviposition behavior of laboratory flies was greater than that of wild flies.*

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**KEY WORDS:** *Anastrepha ludens*; fruit fly; grapefruit; attraction; oviposition; experience.

### **INTRODUCTION**

The Mexican fruit fly, *Anastrepha ludens* (Loew), is a serious pest of citrus and mangoes in Mexico and Central America. In the United States, its detection triggers quarantine restrictions for exportation of commercial fruit

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and control or eradication programs to reduce or eliminate populations from infested areas. Because of the importance of the Mexican fruit fly, various governmental agencies in the United States have invested heavily in research to understand and control this pest.

One avenue of research that has received little attention is the question of host fruit preference. Norrbom and Kim (1988) stated that over 60 hosts have been reported for the Mexican fruit fly, of which about 35 are well-documented field-infested hosts. Among commercial citrus, grapefruit (*Citrus paradisi* MacFayden) seems to be the preferred host of this fly as indicated by high infestation rates in grapefruit orchards compared with orchards of other citrus species (Baker *et al.*, 1944). The reasons for this apparent preference are not known but could include differences in attractiveness, acceptance for oviposition, larval survival, and orchard microhabitats.

Attractiveness, acceptance, and survival are very different measures of preference and are probably mediated by at least some different physical and chemical characteristics of fruit. Of the three, attractiveness and acceptance probably stem from some of the same fruit characters. For example, fruit color, shape, size, and aroma all play roles in eliciting attraction to and acceptance of host fruit in several species of fruit flies (Fletcher and Prokopy, 1991). However, attraction at close range in nature may rely more on visual than chemical characteristics because odor plumes arising from many fruit at the same time on the same tree become indiscrete (Prokopy *et al.*, 1987). Another factor that has proven important in attractiveness and acceptance of a particular host fruit is prior experience with that or other fruit. The effects of experience with host fruit have been studied extensively in apple maggot and, to a lesser degree, in several other fruit flies. In most cases, experience with a particular host increased the preference for that host over novel (not experienced) ones, mainly by decreasing acceptance of the novel hosts, compared with responses of naive flies (Fletcher and Prokopy, 1991).

The research reported here was initiated to learn why grapefruit is infested preferentially over other commercial citrus hosts. We pursued three objectives. Our first objective was to determine if Mexican fruit flies are attracted to grapefruit by its odor. Our second objective was to find the source of the attractive chemicals in the fruit. For this, we followed the work of Papaj *et al.* (1989) in that grapefruit were mechanically wounded to localize the origin within the fruit of chemicals attractive to oviposition-ready females. Our third objective was to determine if experience with grapefruit affected its attractiveness and acceptance to the flies. These objectives were investigated in a single experiment in which attraction and oviposition behavior of flies with or without fruit experience were tested using fruit with different levels of mechanical wounding. The experiment was carried out in a wind tunnel using both laboratory strain and wild Mexican fruit flies.

## MATERIALS AND METHODS

### Insects and Handling Methods

Laboratory stock of *A. ludens* was started in 1997 from 2000 pupae collected from yellow chapote fruit (*Sargentia greggii* S. Wats.) (Rutaceae), a native host from the Montemorelos area of Nuevo Leon in northeastern Mexico. Flies from this culture were reared on artificial medium after egg collection in wax domes. Wild flies were obtained from grapefruits and sour oranges (*C. aurantium* L.) collected in orchards from the Montemorelos area. Adults of both strains were held in Plexiglas cages (20.5 × 20.5 × 20.5 cm) with screened tops containing a diet mixture of sugar and yeast hydrolysate, with water supplied separately. Half of the cages also contained a ripe (yellow peel) grapefruit of variety Rio Red obtained from an orchard located near the laboratory in Weslaco, Texas. Laboratory-strain and wild-strain flies were used in experiments when 9–19 and 10–23 days old, respectively. This age range was based on observations of oviposition behavior by both strains of flies in holding cages containing grapefruit. Also, Dickens *et al.* (1982) demonstrated that sexual maturation and mating occurs by 9 days posteclosion in laboratory-reared Mexican fruit flies. Laboratory conditions where flies were housed were 22 ± 2°C and 50 ± 20% relative humidity, with a photophase of 0630 to 1930 h provided by fluorescent lights. Experiments were conducted between 0900 and 1700 h.

### Wind-Tunnel Experiment

Bioassays were conducted in a Plexiglas wind tunnel (0.3 × 0.3 × 1.2 m) screened on each end to allow airflow. The downwind end contained a baffle system to create uniform airflow through the chamber. Air was pulled through the chamber at 0.4 m/s by an exhaust fan connected to the downwind end. The top of the chamber had two circular openings (12.8-cm diameter) with Plexiglas covers, located at each end of the chamber, to allow easy access to the chamber's interior. A 75-W Soft White light bulb (General Electric Co., Cleveland, OH) in a reflecting lamp was positioned 17 cm above the downwind end of the chamber. The purpose of this light was to use the flies' positive phototactic reaction to minimize random flying into the upwind end of the chamber, which could result in accidental landings on the fruit or the ball. Overhead lighting was provided by two banks each of four fluorescent Cool White lights (F40CW; General Electric).

Ripe Rio Red-variety grapefruit from the Weslaco orchard were used as test fruit in wind-tunnel bioassays. Some grapefruit were damaged before

bioassays by making shallow cuts with a razor blade into the flavedo and albedo (peel cut). A circular piece of the rind and pulp measuring 2.5 cm in diameter was removed from other grapefruit so that volatiles from both the peel and the pulp were present in the aroma (pulp cut). Volatiles from peel-cut and pulp-cut fruit differed as determined by human olfaction. A set of three grapefruit (undamaged, peel cut, pulp cut) was used for an entire replication without refreshing the wounds, then discarded. Grapefruit were washed with water before each trial to remove any chemicals left by flies in the previous trial. A yellow plastic 8-cm-diameter ball (Robacker, 1992) was used in place of grapefruit in some of the bioassays as a control.

About 24 flies (11 or 12 of each sex) were transferred into pint-size, cylindrical paper cups with screen tops 24 h prior to testing. Sugar, yeast hydrolysate, and water were provided with the cups. The experiment was conducted as a random series of 16 fruit  $\times$  fly type treatments, each tested with a different cup of flies. Treatments were all combinations of four fruit types (yellow ball, undamaged grapefruit, peel-cut grapefruit, and pulp-cut grapefruit), two strains (laboratory and wild), and two experience levels (experienced, i.e., held with grapefruit from eclosion, or naive). To conduct a trial, a grapefruit or yellow ball was hung from the opening in the upwind end of the chamber, and one cup of flies was placed under the downwind opening. Flies were allowed 5 min to leave the cup and respond to the fruit or ball. Upwind movement was scored if flies passed a point two-thirds of the distance from the release cup to the fruit or ball. Landing was scored for either landing or walking onto the fruit or ball. Attempted oviposition was scored for ovipositor probing whether or not penetration was achieved. No attempt was made to recover eggs. Twenty-seven replications of the experiment were conducted. However, several replications were conducted in which one or two of the grapefruit types were left out because not enough flies were available to test all treatments.

### Statistical Analyses

All behaviors except oviposition propensity were tested by factorial analysis of variance with replication [SuperANOVA (Abacus Concepts, 1989)]. Proportions of flies that moved upwind, landed on the fruit or ball, or attempted oviposition on fruit or the walls of the wind tunnel were transformed by arcsin of the square root (Snedecor and Cochran, 1967) before statistical analyses. Proportions of 0 were replaced with  $1/4n$  before transformation. Main effects and interactions of fruit type, strain, and experience were calculated for each fly behavior. Most analyses were done using reduced models by either pooling data for some factors or removing data

for responses to one or more treatments. In effect, these procedures sometimes resulted in removal of whole factors. Additional nonfactorial analyses were performed to determine the overall treatment effect for the four strain  $\times$  experience treatments. These reduced models were used to make the most appropriate comparisons for each effect tested. Separate analyses were conducted for males and females. Means separations were conducted using Fisher's protected least significant difference method (Snedecor and Cochran, 1967). Oviposition propensity (percentage of females that attempted oviposition after landing on a fruit) was analyzed by chi-square tests of single classifications with equal expectations, i.e., that the oviposition propensity did not differ for yellow balls and the three grapefruit treatments (Snedecor and Cochran, 1967).

RESULTS

Responses of naive laboratory strain females to grapefruit with different levels of mechanical wounding are listed in Table I (reduced model: wild strain and experience removed). More females moved upwind toward ( $P < 0.01$ ,  $F = 4.3$ ,  $df = 3,71$ ) and landed on ( $P < 0.001$ ,  $F = 9.1$ ,  $df = 3,71$ ) grapefruit with wounds in the peel and pulp than moved toward or landed on undamaged grapefruit or yellow balls. More females attempted oviposition on wounded fruit than on yellow balls ( $P < 0.01$ ,  $F = 4.7$ ,  $df = 3,71$ ). Among females that landed on grapefruit or yellow balls, there were no

**Table I.** Percentages of Mexican Fruit Flies that Exhibited Attraction and Oviposition Behavior in a Wind Tunnel Containing an Undamaged Grapefruit, a Grapefruit with Peel or Pulp Damage, or a Yellow Ball: Laboratory Strain Females Without Experience with Grapefruit<sup>a</sup>

	Moved upwind <sup>b</sup>	Landed on fruit/ball <sup>b</sup>	Attempted to oviposit on fruit/ball <sup>b</sup>	Oviposition propensity on fruit/ball <sup>c</sup>	Attempted to oviposit on wind tunnel <sup>b</sup>
Yellow ball	7.3 a	0.3 a	0.0 a	0	5.1 a
Grapefruit					
Undamaged	7.9 a	1.9 a	1.2 ab	43	4.8 a
Peel cut	13.4 b	6.0 b	4.2 c	71	5.7 a
Pulp cut	13.4 b	6.3 b	3.5 bc	62	5.9 a

<sup>a</sup>Means followed by different letters in the same column are significantly different at the 5% level by Fisher's protected LSD.  
<sup>b</sup>Values are mean percentages of females responding of the total females in the trial. Yellow ball—27 trials, mean = 11.1 females per trial; undamaged grapefruit—25, 11.3; peel cut—25, 11.2; pulp cut—24, 11.7.  
<sup>c</sup>Values are percentages of females responding of females that landed on the fruit/ball. Yellow ball,  $n = 1$  female landed; undamaged grapefruit, 7; peel cut, 17; pulp cut, 16. No significant differences were found by chi-square test of single classifications with equal expectations.

**Table II.** Percentages of Mexican Fruit Flies that Exhibited Attraction and Oviposition Behavior in a Wind Tunnel Containing an Undamaged Grapefruit, a Grapefruit with Peel or Pulp Damage, or a Yellow Ball: Wild-Strain Females Without Experience with Grapefruit<sup>a</sup>

	Moved upwind <sup>b</sup>	Landed on fruit/ball <sup>b</sup>	Attempted to oviposit on fruit/ball <sup>b</sup>	Oviposition propensity on fruit/ball <sup>c</sup>	Attempted to oviposit on wind tunnel <sup>b</sup>
Yellow ball	3.3 a	0.0 a	0.0 a	—	4.3 b
Grapefruit					
Undamaged	6.6 a	0.7 a	0.4 a	50	3.2 b
Peel cut	3.6 a	0.7 a	0.0 a	0	0.5 a
Pulp cut	3.8 a	0.8 a	0.8 a	100	3.7 b

<sup>a</sup>Means followed by different letters in the same column are significantly different at the 5% level by Fisher's protected LSD.

<sup>b</sup>Values are mean percentages of females responding of the total females in the trial. Yellow ball—27 trials, mean = 11.1 females per trial; undamaged grapefruit—25, 11.5; peel cut—25, 11.0; pulp cut—24, 11.3.

<sup>c</sup>Values are percentages of females responding of females that landed on the fruit/ball. Yellow ball,  $n = 0$  females landed; undamaged grapefruit, 2; peel cut, 2; pulp cut, 2. No significant differences were found by chi-square test of single classifications with equal expectations.

significant differences in oviposition propensity. The lack of significance probably occurred because only one female landed on a yellow ball. The number of females to attempt oviposition on the sides of the wind tunnel was not affected by fruit type.

Responses of naive wild females are listed in Table II (reduced model: laboratory strain and experience removed). There were no significant differences in the number of females to move upwind toward, land on, or attempt oviposition on yellow balls or grapefruit of different wounding levels. So few females landed on the grapefruit or yellow balls that the analysis of oviposition propensity had little meaning. Significantly fewer females attempted to oviposit on the wind tunnel when grapefruit with peel wounds were tested ( $P < 0.05$ ,  $F = 3.1$ ,  $df = 3,62$ ).

Responses of experienced laboratory strain females are listed in Table III (reduced model: wild strain and naive removed). Summed over wounding levels, more females moved upwind toward grapefruit than yellow balls ( $P < 0.05$ ,  $F = 3.2$ ,  $df = 3,71$ ). More females landed ( $P < 0.001$ ,  $F = 6.4$ ,  $df = 3,71$ ) and attempted oviposition ( $P < 0.001$ ,  $F = 13.4$ ,  $df = 3,71$ ) on grapefruit with mechanical wounding than on yellow balls or undamaged fruit. More females attempted oviposition on grapefruit with peel wounds than on fruit with pulp wounds. Among females that landed on grapefruit or yellow balls, there was no significant difference in oviposition propensity. The lack of significance probably occurred because only four females landed on a yellow ball. The number of females to attempt oviposition on the wind tunnel was not affected by fruit type.

**Table III.** Percentages of Mexican Fruit Flies that Exhibited Attraction and Oviposition Behavior in a Wind Tunnel Containing an Undamaged Grapefruit, a Grapefruit with Peel or Pulp Damage, or a Yellow Ball: Laboratory-Strain Females with Experience with Grapefruit<sup>a</sup>

	Moved upwind <sup>b</sup>	Landed on fruit/ball <sup>b</sup>	Attempted to oviposit on fruit/ball <sup>b</sup>	Oviposition propensity on fruit/ball <sup>c</sup>	Attempted to oviposit on wind tunnel <sup>b</sup>
Yellow ball	7.9 a	1.2 a	0.0 a	0	0.0 a
Grapefruit					
Undamaged	12.4 ab	2.4 ab	1.0 ab	43	0.0 a
Peel cut	17.6 b	9.9 c	7.9 c	79	0.5 a
Pulp cut	12.1 a	6.8 bc	4.1 b	71	0.0 a

<sup>a</sup>Means followed by different letters in the same column are significantly different at the 5% level by Fisher's protected LSD.  
<sup>b</sup>Values are mean percentages of females responding of the total females in the trial. Yellow ball—27 trials, mean = 11.5 females per trial; undamaged grapefruit—25, 11.5; peel cut—25, 11.4; pulp cut—24, 11.4.  
<sup>c</sup>Values are percentages of females responding of females that landed on the fruit/ball. Yellow ball, *n* = 4 females landed; undamaged grapefruit, 7; peel cut, 29; pulp cut, 19. No significant differences were found by chi-square test of single classifications with equal expectations.

Responses of experienced wild females are listed in Table IV (reduced model: laboratory strain and naive removed). More females moved upwind toward grapefruit than yellow balls (*P* < 0.001, *F* = 6.9, *df* = 3,71). Fruit wounding had no effect. More females landed on grapefruit with pulp wounds than on yellow balls or undamaged grapefruit (*P* < 0.01, *F* = 5.5,

**Table IV.** Percentages of Mexican Fruit Flies that Exhibited Attraction and Oviposition Behavior in a Wind Tunnel Containing an Undamaged Grapefruit, a Grapefruit with Peel or Pulp Damage, or a Yellow Ball: Wild-Strain Females with Experience with Grapefruit<sup>a</sup>

	Moved upwind <sup>b</sup>	Landed on fruit/ball <sup>b</sup>	Attempted to oviposit on fruit/ball <sup>b</sup>	Oviposition propensity on fruit/ball <sup>c</sup>	Attempted to oviposit on wind tunnel <sup>b</sup>
Yellow ball	5.2 a	1.4 a	0.7 a	50	0.8 a
Grapefruit					
Undamaged	10.1 b	1.9 a	1.5 a	80	0.4 a
Peel cut	10.9 b	3.3 ab	1.8 a	56	0.0 a
Pulp cut	14.2 b	6.4 b	4.4 b	71	0.9 a

<sup>a</sup>Means followed by different letters in the same column are significantly different at the 5% level by Fisher's protected LSD.  
<sup>b</sup>Values are mean percentages of females responding of the total females in the trial. Yellow ball—27 trials, mean = 11.5 females per trial; undamaged grapefruit—25, 11.3; peel cut—25, 11.1; pulp cut—24, 11.4.  
<sup>c</sup>Values are percentages of females responding of females that landed on the fruit/ball. Yellow ball, *n* = 4 females landed; undamaged grapefruit, 5; peel cut, 9; pulp cut, 17. No significant differences were found by chi-square test of single classifications with equal expectations.

df = 3,71). More females attempted to oviposit on grapefruit with pulp wounds than on other fruit or yellow balls ( $P < 0.01$ ,  $F = 4.1$ , df = 3,71). Among females that landed on grapefruit or yellow balls, there was no significant difference in oviposition propensity. The number of females to attempt oviposition on the wind tunnel was not affected by fruit type.

Responses of females of the two strains and experience types differed. Summed over experience types, more laboratory-strain (Tables I and III) than wild females (Tables II and IV) moved upwind ( $P < 0.001$ ,  $F = 14.9$ , df = 1,266), landed on grapefruit ( $P < 0.001$ ,  $F = 17.6$ , df = 1,266), and attempted oviposition on fruit ( $P < 0.001$ ,  $F = 12.2$ , df = 1,266) (reduced model: fruit type removed, data for yellow balls removed). Oviposition propensity on grapefruits did not differ between laboratory and wild strains. More laboratory-strain than wild females attempted to oviposit on the wind tunnel ( $P = 0.06$ ,  $F = 3.6$ , df = 1,317) (full model).

Interaction of strain with fruit type was significant for landings ( $P < 0.05$ ,  $F = 3.4$ , df = 2,258) and attempted ovipositions ( $P < 0.001$ ,  $F = 7.9$ , df = 2,258) (full model: data for yellow balls removed). This interaction occurred because laboratory females responded to grapefruit with peel wounds at disproportionately higher rates than wild flies compared with response ratios on undamaged grapefruit or those with pulp wounds.

Summed over strains, more experienced (Tables III and IV) than naive females (Tables I and II) moved upwind ( $P < 0.001$ ,  $F = 14.7$ , df = 1,266), landed on grapefruit ( $P < 0.01$ ,  $F = 9.4$ , df = 1,266), and attempted oviposition on fruit ( $P < 0.01$ ,  $F = 9.2$ , df = 1,266) (reduced model: fruit type removed, data for yellow balls removed). Oviposition propensity on grapefruit did not differ between naive and experienced females. Fewer experienced than naive females attempted to oviposit on the wind tunnel ( $P < 0.0001$ ,  $F = 69.5$ , df = 1,317) (full model).

Interaction of strain with experience was significant for upwind movement by females to grapefruit ( $P < 0.05$ ,  $F = 5.2$ , df = 1,258) (full model: data for yellow balls removed). This effect occurred because experienced laboratory females responded at only slightly higher rates than naive ones, whereas experienced wild females responded at much higher rates than naive ones. Similar results were obtained for landings and ovipositions but the interactions were not significant.

Responses of experienced laboratory strain males are listed in Table V. More males landed on grapefruit with wounds in the pulp than on yellow balls ( $P < 0.001$ ,  $F = 9.1$ , df = 3,71) (reduced model: wild strain and naive removed). Upwind movement toward grapefruit was not significant but the trend was the same as for landings. For naive laboratory males, and naive and experienced wild males, no significant differences were found for responses to grapefruit or yellow balls (data not shown).



**Table V.** Percentages of Mexican Fruit Flies Attracted to an Undamaged Grapefruit, a Grapefruit with Peel or Pulp Damage, or a Yellow Ball in a Wind Tunnel: Laboratory-Strain Males with Experience with Grapefruit<sup>a</sup>

	Moved upwind	Landed on fruit/ball
Yellow ball	4.3 a	0.0 a
Grapefruit		
Undamaged	5.7 a	1.0 ab
Peel cut	5.0 a	0.7 ab
Pulp cut	8.3 a	2.4 b

<sup>a</sup>Values are mean percentages of males responding of the total males in the trial. Yellow ball—27 trials, mean = 11.5 males per trial; undamaged grapefruit—25, 11.6; peel cut—25, 11.1; pulp cut—24, 11.5. Means followed by different letters in the same column are significantly different at the 5% level by Fisher's protected LSD.

Responses of males of the two strains and experience types in trials with grapefruit, summed over degrees of mechanical wounding, are listed in Table VI (nonfactorial ANOVA of fruit type and overall treatment effect for the four strain by experience treatments: data for yellow balls removed). More laboratory-strain than wild flies, summed over experience types, moved upwind toward ( $P < 0.0001$ ,  $F = 29.0$ ,  $df = 1,258$ ) and landed on ( $P < 0.001$ ,  $F = 13.0$ ,  $df = 1,258$ ) grapefruit (full model: data for yellow balls removed). Experience with grapefruit did not affect upwind movements by males ( $P = 1.0$ ,  $F = 0.0$ ,  $df = 1,258$ ) (full model: data for yellow balls removed). Summed over strains, more experienced than naive males landed on grapefruit ( $P < 0.05$ ,  $F = 4.1$ ,  $df = 1,258$ ) (full model: data for yellow balls removed). Experienced laboratory-strain males landed

**Table VI.** Percentages of Males of Two Strains of Mexican Fruit Flies, With or Without Previous Experience with Grapefruit, Attracted to a Grapefruit in a Wind Tunnel<sup>a</sup>

	Moved upwind	Landed on fruit
Lab		
No experience	6.7 b	0.5 a
Experience	6.3 b	1.4 b
Wild		
No experience	2.3 a	0.0 a
Experience	2.7 a	0.1 a

<sup>a</sup>Values are mean percentages of males responding out of the total males in the trial. Lab, no experience—74 trials, 11.3 males per trial; lab, experience—74, 11.4; wild, no experience—74, 11.2; wild, experience—74, 11.0. Means followed by different letters in the same column are significantly different at the 5% level by Fisher's protected LSD.

on grapefruit more often than wild males or naive laboratory-strain males ( $P < 0.001$ ,  $F = 6.3$ ,  $df = 3,264$ ) (nonfactorial ANOVA of fruit type and overall treatment effect for the four strain  $\times$  experience treatments: data for yellow balls removed). No interactions were significant.

## DISCUSSION

Wild-strain female Mexican fruit flies that had no prior experience with fruit were not attracted to grapefruit aroma in this work (Table II). This suggests that the preference for grapefruit over other commercial citrus fruits manifested as higher infestation rates in the field (Baker *et al.*, 1944) is not due to innate attractiveness of grapefruit aroma to oviposition-ready females. Naive laboratory-strain females were attracted to grapefruits (Table I). This suggests that laboratory-strain flies are selected to be opportunists capable of responding to unfamiliar fruit in an unnatural arena.

Numerous papers have addressed the issue of attraction of oviposition-ready females to host fruits. Evidence that host fruit odor is attractive to fruit flies searching for oviposition sites is so strong that it could be stated as a general principle (Fletcher and Prokopy, 1991; Jang and Light, 1996). However, most of the studies have been done with either laboratory-strain flies or wild flies with host fruit experience. Relatively few studies have demonstrated that wild, gravid, tephritid flies with no previous experience with host fruit are attracted to odor of host fruit, principally because few have been undertaken for this purpose. Studies that have demonstrated this phenomenon include those by Averill *et al.* (1988), Landolt and Reed (1990), Prokopy *et al.* (1990a), Prokopy and Vargas (1996), and Katsoyannos *et al.* (1997).

Females experienced with grapefruit, whether laboratory or wild strain, were attracted to grapefruit in our work (Tables III and IV). Naive wild females were not attracted to grapefruit and naive laboratory females were attracted only weakly compared with experienced laboratory females. Our results are consistent with increased attraction to and usage of experienced fruit types over novel fruit types demonstrated in Mediterranean fruit fly (*Ceratitis capitata* Wiedemann) and fruit flies of the genera *Rhagoletis* and *Bactrocera* (Cooley *et al.*, 1986; Prokopy *et al.*, 1990a,b, 1991, 1993; Fletcher and Prokopy, 1991; Averill *et al.*, 1996).

In general, more females, both naive and grapefruit-experienced, were attracted to grapefruit with mechanical wounding of peels or pulp compared with undamaged fruit (Tables I, III, and IV). Similar results were obtained by Papaj *et al.* (1989) with *C. capitata* and Prokopy *et al.* (1990a) with *Bactrocera dorsalis* Hendel. Peel wounds and pulp wounds were about equally attractive in our work. This contrasts with results of Papaj *et al.* (1989), who found that pulp wounds, but not shallow peel wounds, enhanced

landing by oviposition-ready, female, Mediterranean fruit flies. Also, Katsoyannos *et al.* (1997) showed that both male and female Mediterranean fruit flies were attracted to volatiles from wounded pulp of oranges but only males were attracted to chemicals from flavedo. Our results could be explained on the basis that only peel chemicals were important because both types of wounds have damage to the peel or that pulp chemicals had the same effect as peel chemicals. In either case, the most likely explanation for the enhanced attraction to wounded fruit is increased emission of fruit volatiles, for both innate attraction of naive laboratory females and learned attraction by experienced females. Insect visual acuity is poor compared with that of vertebrates (Chapman, 1971). As such, the wounds, especially the peel wounds that consist of small cuts in the peel, would not be readily perceived visually by the flies. Our experimental protocol was not designed to study the importance of visual stimuli, however, both visual and chemical stimuli from host fruit are known to be involved in innate and learned attraction of fruit flies to the fruit (Papaj and Prokopy, 1986; Prokopy *et al.*, 1990a, 1994; Fletcher and Prokopy, 1991; Henneman and Papaj, 1999).

We found no evidence that oviposition propensity on grapefruit was affected by either fruit wounding or prior experience with grapefruit (Tables I–IV). In fact, our data did not even demonstrate that oviposition propensity was greater on grapefruit than on yellow balls, probably because too few flies landed on yellow balls to make the analyses meaningful. Again, our data contrast with those of Papaj *et al.* (1989), who found that the oviposition propensity of Mediterranean fruit flies was greater on wounded oranges than on undamaged ones, suggesting that increased fruit volatiles enhanced oviposition. Further, they showed that most flies bored into or very near the wounds and hypothesized that laying eggs into deep wounds increased larval survival because larvae emerged in or very near the pulp, not in toxic oils in the peel. We did not observe Mexican fruit flies attempting oviposition into pulp wounds, and the proximity of oviposition bouts to wounds was not recorded. Papers other than Papaj *et al.* (1989) have also demonstrated the importance of host odor in stimulating fruit flies to oviposit (Levinson and Haisch, 1984; Chiu, 1990; Jang and Light, 1991). Perhaps with longer observation periods, we would have observed more landings on yellow balls and higher oviposition propensity on grapefruit. However, our study was designed primarily to investigate attraction, and brief trial times were necessary to minimize random landing on grapefruit and yellow balls.

We considered two possible explanations for why oviposition propensity on grapefruit by naive and experienced females did not differ. First, experience may have had no effect on acceptance of fruit for oviposition. However, experience is known to increase acceptance in some flies (Prokopy *et al.*, 1982; Cooley *et al.*, 1986; McDonald, 1986; Papaj and Prokopy, 1988;

Fletcher and Prokopy, 1991). Alternatively, experience may have enhanced acceptance but the enhancement may have been offset by an effect of greater egg load in naive females that stimulated them to dump eggs on any substrate. Higher egg load in naive females is possible because they did not have access to fruit to lay eggs prior to tests. However, we also observed that naive females laid more eggs than experienced females inside their holding cages, mostly in the cloth sleeves. Thus, the status of their egg load during tests is unknown and we cannot determine if experience had any effect on acceptance of fruit for oviposition.

The propensity to attempt oviposition on the sides of the wind tunnel was greatly reduced if flies had previous experience with grapefruit (Tables III and IV vs I and II). As with the propensity to attempt oviposition in grapefruit, we could not determine if this was due to learning by experienced flies or high egg load in naive flies. However, the results are congruent with studies of other fruit flies in which experience with a host fruit decreased acceptance of novel fruit (Cooley *et al.*, 1986; Papaj and Prokopy, 1986; Prokopy *et al.*, 1986; Fletcher and Prokopy, 1991) or plastic oviposition spheres (Prokopy *et al.*, 1990b).

Responses of males to grapefruit were weak compared with responses of females. As with females, however, laboratory strain males were more responsive than wild males to grapefruit and males with grapefruit experience were more responsive than naive males (Tables V and VI).

The lack of response by naive males in our work brings up the question of whether males of any fruit flies are innately attracted specifically to host fruit odor. Very few studies have addressed this issue. As in our work, Prokopy and Vargas (1996) were unable to demonstrate attraction of wild, naive Mediterranean fruit fly males to odor of coffee, a natural host of the fly. However, Katsoyannos *et al.* (1997) showed attraction of wild, naive males of this species to both flavedo and pulp chemicals from oranges. Prokopy *et al.* (1989) demonstrated that naive, wild apple maggot males spent more time on fruit when released onto hawthorn, a native host, than onto apple, an acquired host. However, actual attraction to either fruit was not studied and the possible role of host odor also was not elucidated.

Attraction of naive, laboratory-strain males to host fruit odors has been reported (Fein *et al.*, 1982; Robacker *et al.*, 1990; Prokopy and Vargas, 1996; Nigg *et al.*, 1994), although it could not be demonstrated in other studies (Chiu, 1990; Cornelius *et al.*, 2000). Also, host fruit odors have been shown to attract wild male fruit flies in the field (Prokopy *et al.*, 1973; Reissig *et al.*, 1982; Cornelius *et al.*, 2000). Again, male attraction to host odor could not be demonstrated in all cases (Prokopy and Vargas, 1996). As with our results, most studies have shown that attraction of male tephritids to host fruit odor is less than that of females.

Some cases of attraction of males to host odors may represent food foraging behavior of hungry males. Evidence is that food deprivation enhanced attraction of males to the odor of a fermented host in the Mexican fruit fly (Robacker *et al.*, 1990). As such, there is no reason why hosts should be more attractive than nonhosts with similar nutritional value. Also, males captured in field tests may have been experienced with fruit odors and formed associations between the odors and food. Prokopy *et al.* (1989) showed that experience with apple or hawthorn fruit increased preference by apple maggot males for the experienced fruit. Males may also respond to host fruit odor as a means of finding females. This is a possibility in our work because females were present in the cages when males were exposed to grapefruit. However, Prokopy *et al.* (1989) were unable to demonstrate that experience with females on a particular fruit type increased the preference for that fruit more so than the preference gained without females. Evidence that males learn to search for females on host fruit comes from studies that have shown that males do not distinguish colors of ripe versus immature fruit until they have experienced females on the ripe fruit (Sivinski, 1990; Henneman and Papaj, 1999).

We found no evidence in this work to explain why Mexican fruit flies infest grapefruit at higher rates than other commercial citrus in the field. In fact, wild females were not innately attracted to the odor of grapefruit in these experiments. Future research will address the question of whether or not wild Mexican fruit flies are innately attracted to other citrus including the yellow chapote, a preferred natural host.

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